SLAVERY IN ANTS

Certain species of ants raid the nests of other species for ants to work in their own nest. Some raiding species have become so specialized that they are no longer capable of feeding themselves

by Edward O. Wilson

The institution of slavery is not unique to human societies. No fewer than 35 species of ants, constituting six independently evolved groups, depend at least to some extent on slave labor for their existence. The techniques by which they raid other ant colonies to strengthen their labor force rank among the most sophisticated behavior patterns found anywhere in the insect world. Most of the slave-making ant species are so specialized as raiders that they starve to death if they are deprived of their slaves. Together they display an evolutionary descent that begins with casual raiding by otherwise free-living colonies, passes through the development of full-blown warrior societies and ends with a degeneration so advanced that the workers can no longer even conduct raids.

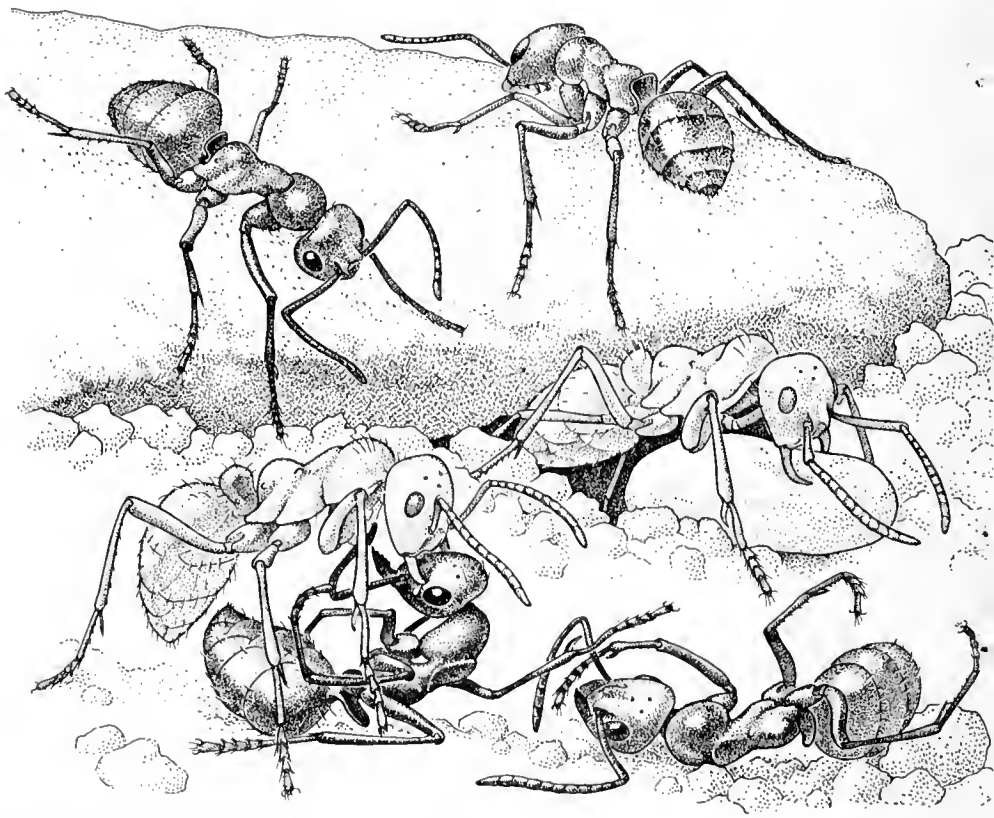
Slavery in ants differs from slavery in human societies in one key respect: the ant slaves are always members of other completely free-living species that themselves do not take slaves. In this regard the ant slaves perhaps more closely resemble domestic animals—except that the slaves are not allowed to reproduce and they are equal or superior to their captors in social organization.

The famous Amazon ants of the genus *Polyergus* are excellent examples of advanced slave makers. The workers are strongly specialized for fighting. Their mandibles, which are shaped like miniature sabers, are ideally suited for puncturing the bodies of other ants but are poorly suited for any of the routine tasks that occupy ordinary ant workers. Indeed, when *Polyergus* ants are in their home nest their only activities are begging food from their slaves and cleaning themselves ("burnishing their ruddy armor," as the entomologist William Morton Wheeler once put it).

When *Polyergus* ants launch a raid, however, they are completely transformed. They swarm out of the nest in a solid phalanx and march swiftly and directly to a nest of the slave species. They destroy the resisting defenders by puncturing their bodies and then seize and carry off the cocoons containing the pupae of worker ants.

When the captured pupae hatch, the workers that emerge accept their captors as sisters; they make no distinction between their genetic siblings and the *Polyergus* ants. The workers launch into the round of tasks for which they have been genetically programmed, with the slave makers being the incidental beneficiaries. Since the slaves are members of the worker caste, they cannot reproduce. In order to maintain an adequate labor force, the slave-making ants must periodically conduct additional raids.

It is a remarkable fact that ants of slave-making species are found only in cold climates. Although the vast majority of ants live in the Tropics and the



RAID BY SLAVE-MAKING AMAZON ANTS of the species *Polyergus rufescens* (*light color*) against a colony of the slave species *Formica fusca* (*dark color*) is depicted. The *fusca* ants make their nest in dry soil under a stone. The raiding Amazon ants kill resisting

warm Temperate zones, not a single species of those regions has been implicated in any activity remotely approaching slavery. Among the ants of the colder regions this form of parasitism is surprisingly common. The colonies of many slave-making species abound in the forests of the northern U.S., and ant-slave raids can be observed in such unlikely places as the campus of Harvard University.

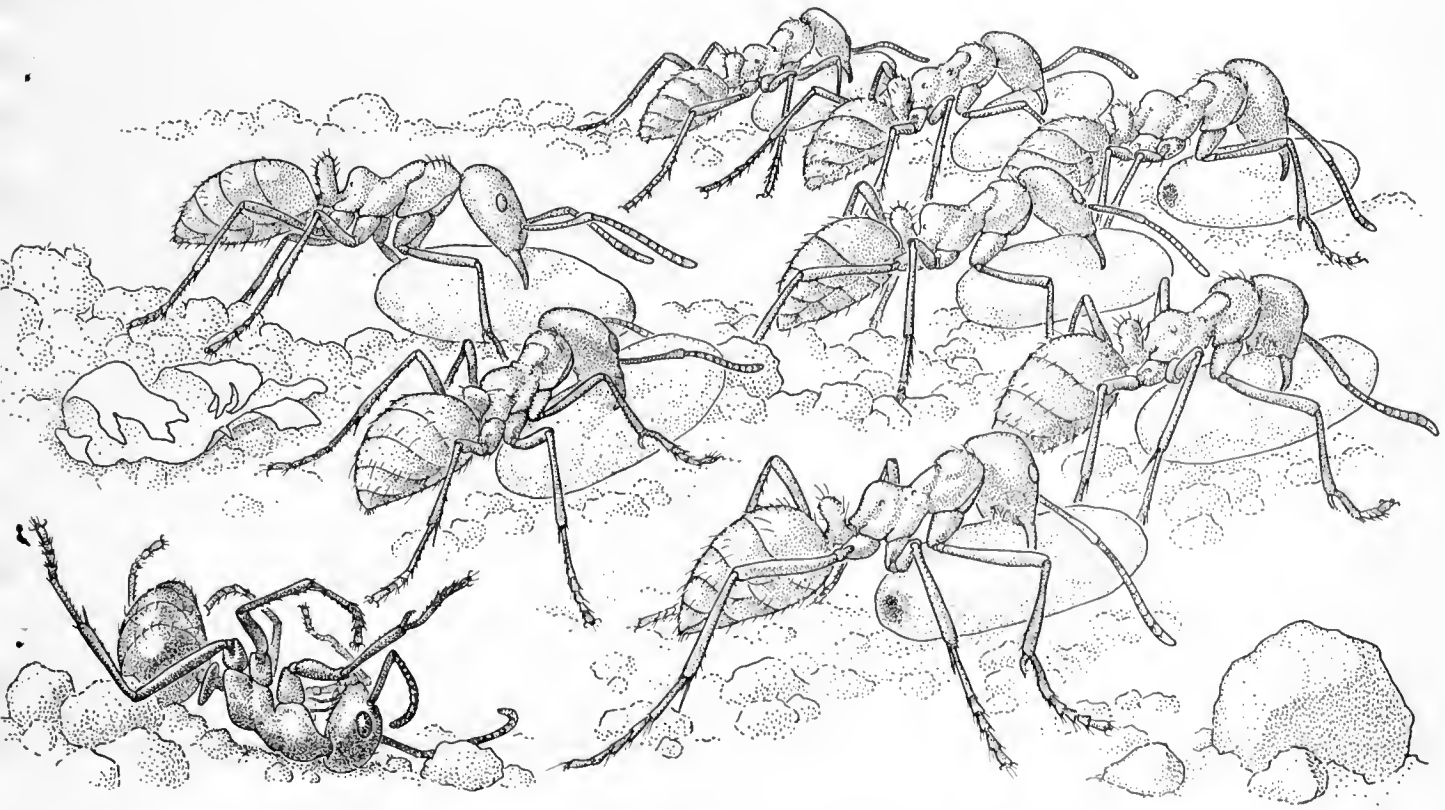
The slave raiders obey what is often called Emery's rule. In 1909 Carlo Emery, an Italian myrmecologist, noted that each species of parasitic ant is genetically relatively close to the species it victimizes. This relation can be profitably explored for the clues it provides to the origin of slave making in the evolution of ants. Charles Darwin, who was fascinated by ant slavery, suggested that the first step was simple predation: the ancestral species began by raiding other kinds of ants for food, carrying away their immature forms in order to be able to devour them in the home nest. If a few pupae could escape that fate long enough to emerge as workers, they might be accepted as nestmates and thus join the labor force. In cases where the captives subsequently proved to be more valuable as workers than as food, the raiding species would tend to evolve into a slave maker.

Although Darwin's hypothesis is attractive, I recently obtained evidence that territorial defense rather than food is the evolutionary prime mover. I brought together in the Harvard Museum of Comparative Zoology different species of *Leptothorax* ants that normally do not depend on slave labor. When colonies were placed closer together than they are found in nature, the larger colonies attacked the smaller ones and drove away or killed the queens and workers. The attackers carried captured pupae back to their own nests. The pupae were then allowed by their captors to develop into workers. In the cases where the newly emerged workers belonged to the same species, they were allowed to remain as active members of the colony. When they belonged to a different *Leptothorax* species, however, they were executed in a matter of hours. One can easily imagine the origin of slave making by the simple extension of this territorial behavior to include tolerance of the workers of related species. The more closely related the raiders and their captives are, the more likely they are to be compatible. The result would be in agreement with Emery's rule.

One species that appears to have just crossed the threshold to slave making is *Leptothorax duloticus*, a rare ant that so far has been found only in certain localities in Ohio, Michigan and Ontario. The anatomy of the worker caste is only slightly modified for slave-making behavior, suggesting that in evolutionary terms the species may have taken up its parasitic way of life rather recently.

In experiments with laboratory colonies I was able to measure the degree of behavioral degeneration that has taken place in *L. duloticus*. Like the Amazon ants, the *duloticus* workers are highly efficient at raiding and fighting. When colonies of other *Leptothorax* species were placed near a *duloticus* nest, the workers launched intense attacks until all the pupae of the other species had been captured.

In the home nest the *duloticus* workers were inactive, leaving almost all the ordinary work to their captives. When the slaves were temporarily taken away from them, the workers displayed a dramatic expansion in activity, rapidly taking over most of the tasks formerly carried out by the slaves. The *duloticus* workers thus retain a latent capacity for working, a capacity that is totally lack-

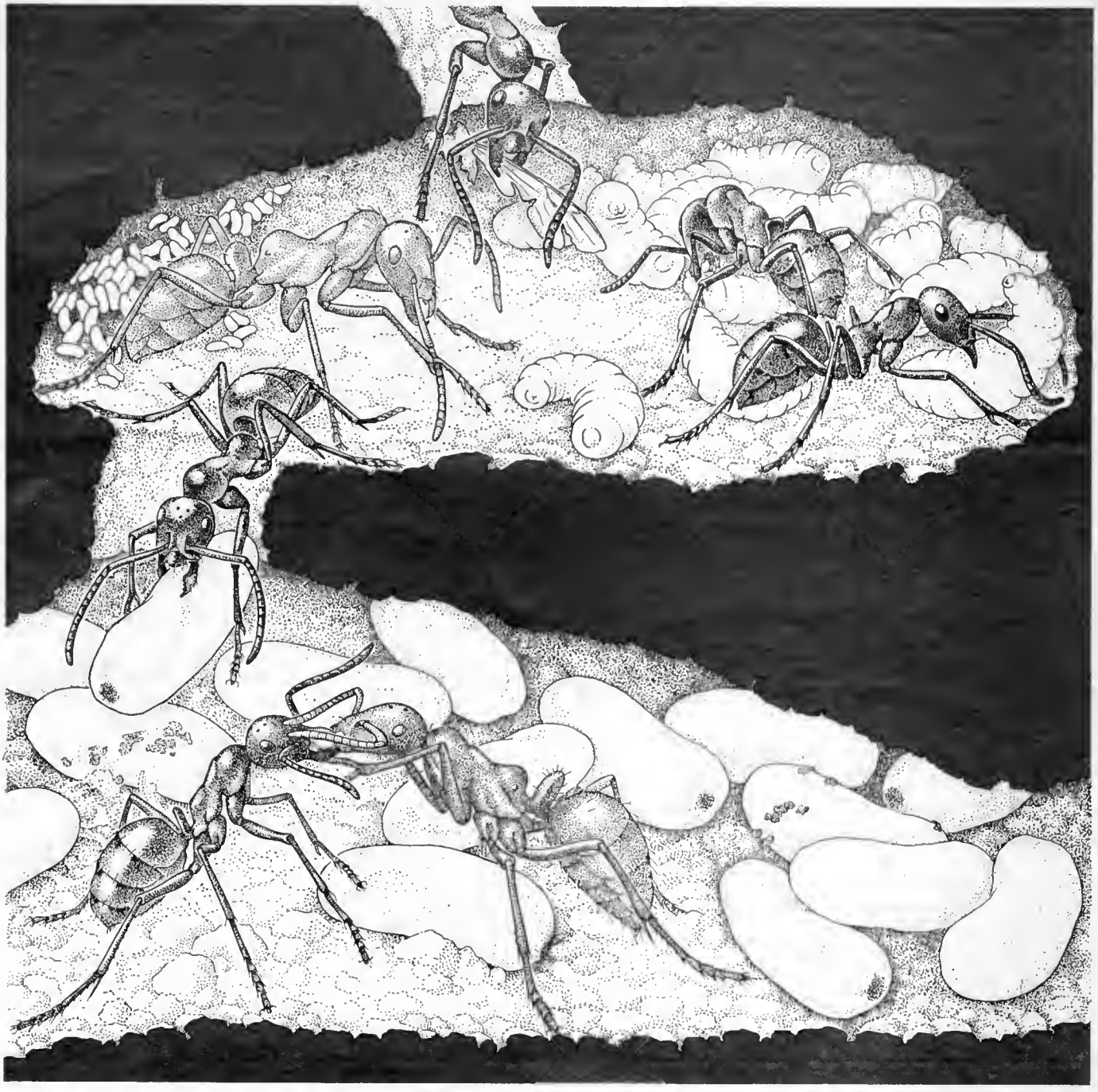


fusca workers by piercing them with their saberlike mandibles. Most of the Amazon ants are transporting cocoons containing the pupae of *fusca* workers back to their own nest. When the workers emerge from the cocoons, they serve as slaves. Two dead *fusca* workers that resisted lie on the ground. Two other workers have retreated to upper surface of the rock over the nest's entrance.

ing in more advanced species of slave-making ants.

The *duloticus* workers that had lost their slaves did not, however, perform their tasks well. Their larvae were fed at infrequent intervals and were not groomed properly, nest materials were carried about aimlessly and were never placed in the correct positions, and an inordinate amount of time was spent collecting and sharing diluted honey. More important, the slaveless ants lacked one behavior pattern that is essential for the survival of the colony: foraging for dead insects and other solid food. They even ignored food placed in their path. When the colony began to display signs of starvation and deterioration, I returned to them some slaves of the species *Leptothorax curvispinosus*. The bustling slave workers soon put the nest back in good order, and the slave makers just as quickly lapsed into their usual indolent ways.

Not all slave-making ants depend on brute force to overpower their victims. Quite by accident Fred E. Regnier of Purdue University and I discovered that some species have a subtler strategy. While surveying chemical substances used by ants to communicate alarm and to defend their nest, we encountered two slave-making species whose substances differ drastically from those of all other ants examined so far. These ants, *Formica subintegra* and *Formica pergandei*, produce remarkably large quantities of decyl, dodecyl and tetradecyl acetates. Further investigation of *F. subintegra*



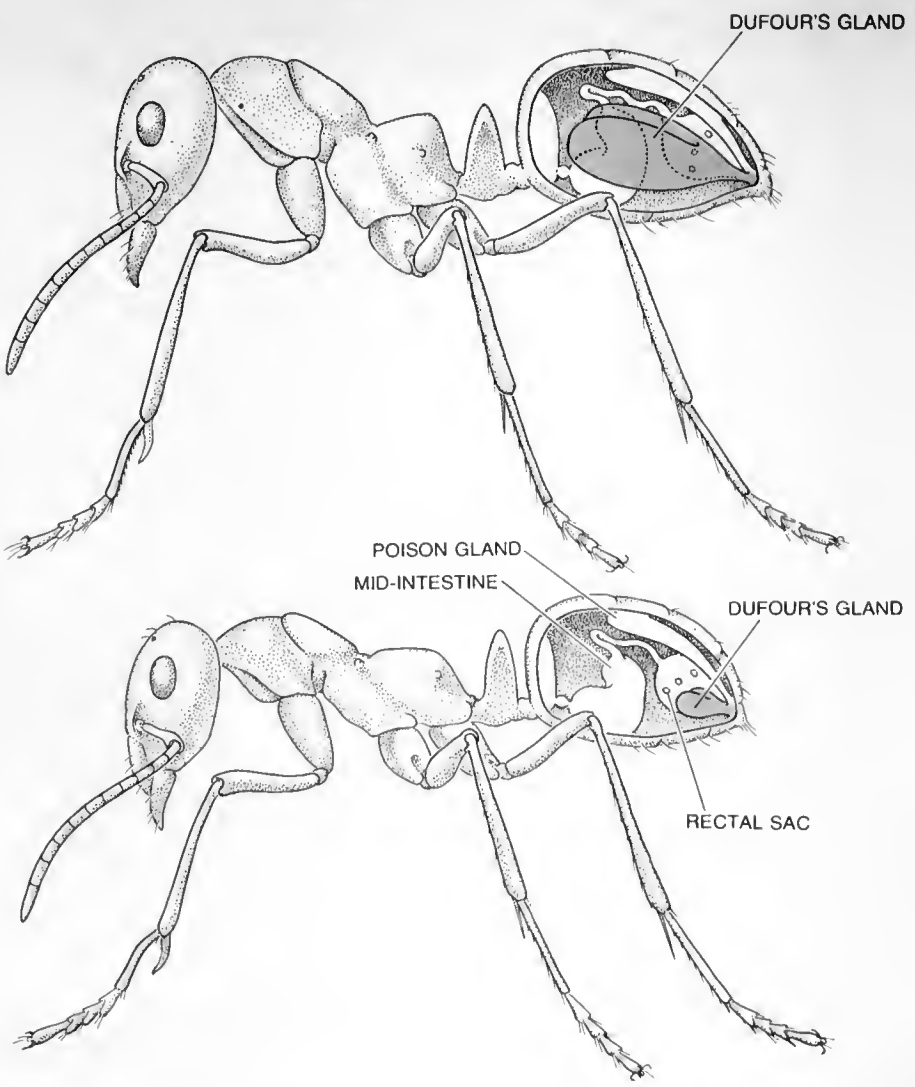
INTERIOR VIEW OF THE HOME NEST of a colony of Amazon ants shows *Formica fusca* slaves (*dark color*) performing all the housekeeping labor. At top center one of the slaves brings a fly wing into the nest for food. Other slave workers care for the small eggs, grublike larvae and cocoon-enclosed pupae of their captors. During the raiding season some of the pupae are likely to be those of *fusca* workers. The slave makers (*light color*) can do nothing more than groom themselves (*upper left*). In order to eat, the Amazon ants must beg slave workers to regurgitate liquid droplets for them (*lower left*). These ant species are found in Europe.

revealed that the substances are sprayed at resisting ants during slave-making raids. The acetates attract more invading slave makers, thereby serving to assemble these ants in places where fighting breaks out. Simultaneously the sprayed acetates throw the resisting ants into a panic. Indeed, the acetates are exceptionally powerful and persistent alarm substances. They imitate the compound undecane and other scents found in slave species of *Formica*, which release these substances in order to alert their nestmates to danger. The acetates broadcast by the slave makers are so much stronger, however, that they have a long-lasting disruptive effect. For this reason Regnier and I named them "propaganda substances."

We believe we have explained an odd fact first noted by Pierre Huber 165 years ago in his pioneering study of the European slave-making ant *Formica sanguinea*. He found that when a colony was attacked by these slave makers, the survivors of the attacked colony were reluctant to stay in the same neighborhood even when suitable alternative nest sites were scarce. Huber observed that the "ants never return to their besieged capital, even when the oppressors have retired to their own garrison; perhaps they realize that they could never remain there in safety, being continually liable to the attacks of their unwelcome visitors."

Regnier and I were further able to gain a strong clue to the initial organization of slave-making raids. We had made a guess, based on knowledge of the foraging techniques of other kinds of ants, that scout workers direct their nestmates to newly discovered slave colonies by means of odor trails laid from the target back to the home nest. In order to test this hypothesis we made extracts of the bodies of *F. subintegra* and of *Formica rubicunda*, a second species that conducts frequent, well-organized raids through much of the summer. Then at the time of day when raids are normally made we laid artificial odor trails, using a narrow paintbrush dipped in the extracts we had obtained from the ants. The trails were traced from the entrances of the nest to arbitrarily selected points one or two meters away.

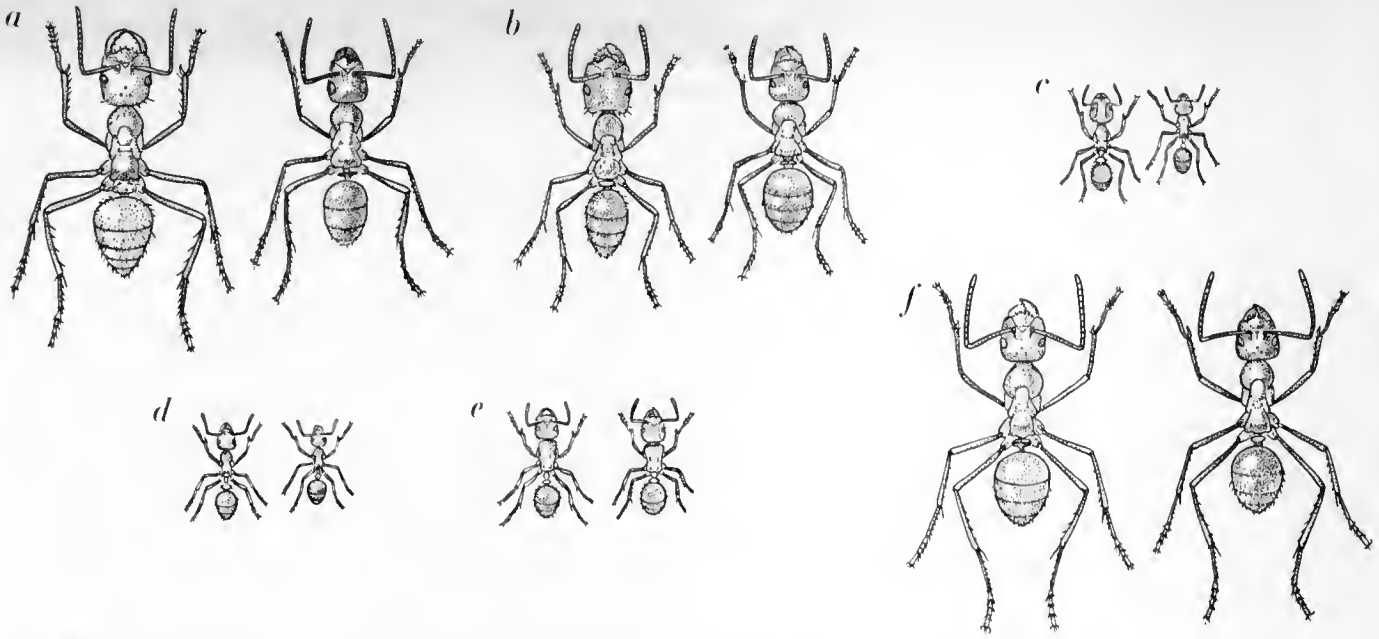
The results were dramatic. Many of the slave-making workers rushed forth, ran the length of the trails and then milled around in confusion at the end. When we placed portions of colonies of the slave species *Formica subsericea* at the end of some of the trails, the slave makers proceeded to conduct the raid in a manner that was apparently the same in every respect as the raids initiated by trails laid by their own scouts. Studies of the slave-making species *Polyergus lucidus* and *Harpagoxenus americanus* by Mary Talbot and her colleagues at Lindenwood College provide independent evidence that raids are organized by the laying of odor trails to target nests; indeed, this form of communication may be widespread among slave-making ants.



DUFOUR'S GLAND, which produces substances that serve as communication scents among ants, is much larger in the slave-making species *Formica subintegra* (*top*) than in the slave species *F. subsericea* (*bottom*). The *subsericea* ant releases its scent to alert its nestmates to the presence of danger. The *subintegra* sprays its secretions at resisting ants during slave raids. The secretions are so strong that they create panic in the colony being attacked.

The evolution of social parasitism in ants works like a ratchet, allowing a species to slip further down in parasitic dependence but not back up toward its original free-living existence. An example of nearly complete behavioral degeneration is found in one species of the genus *Strongylognathus*, which is found in Asia and Europe. Most species in this genus conduct aggressive slave-making raids. They have characteristic saber-shaped mandibles for killing other ants. The species *Strongylognathus testaceus*, however, has lost its warrior habits. Although these ants still have the distinctive mandibles of their genus, they do not conduct slave-making raids. Instead an *S. testaceus* queen moves into the nest of a slave-ant species and lives alongside the queen of the slave species. Each queen lays eggs that develop into workers, but the *S. testaceus* offspring do no work. They are fed by workers of the slave species. We do not know how the union of the two queens is formed in the first place, but it is likely that the parasitic queen simply induces the host colony to adopt her after her solitary dispersal flight from the nest of her birth.

Thus *S. testaceus* is no longer a real slave maker. It has become an advanced social parasite of a kind that commonly infests other ant groups. For example,



RESEMBLANCE of slave maker and slave was noted by an Italian myrmecologist, Carlo Emery, in 1909. In each pair of ants shown here the slave maker is on the left and the slave on the right. The species depicted are (*a*) *Polyergus rufescens* and *Formica fusca*, (*b*) *Rossomyrmex proformicarum* and *Proformica nasutum*, (*c*) *Harpagoxenus americanus* and *Leptothorax curvispinosus*, (*d*) *L. duloticus* and *L. curvispinosus*, (*e*) *Strongylognathus alpinus* and *Tetramorium caespitum* and (*f*) *F. subintegra* and *F. subsericea*.

many species of ant play host to parasites such as beetles, wasps and flies, feeding them and sheltering them [see "Communication between Ants and Their Guests," by Bert Hölldobler; SCIENTIFIC AMERICAN, March, 1971].

Does ant slavery hold any lesson for our own species? Probably not. Human slavery is an unstable social institution that runs strongly counter to the moral systems of the great majority of human societies. Ant slavery is a genetic adaptation found in particular species that cannot be judged to be more or less successful than their non-slave-making counterparts. The slave-making ants offer a clear and interesting case of behavioral evolution, but the analogies with human behavior are much too remote to allow us to find in them any moral or political lesson.

COLONY OF ANTS housed in a glass tube consists of the rare species *Leptothorax duloticus* and a slave species, *L. curvispinosus*. The *duloticus* ant, found in Ohio, Michigan and Ontario, has only recently become a slave maker. One of the *duloticus* workers can be seen in the center of the photograph; below it are three slave workers. The white objects are immature forms of both species. When the slave workers are removed, the *duloticus* workers attempt to carry out necessary housekeeping tasks but do so poorly.